Chapter 21

The Millipede Faunas of Two British Limestone Woods

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Introduction

Samples from the floor of two woods, both on carboniferous limestone, one in Wales and one in Derbyshire, have been taken periodically since 1968, and the animals extracted by Tullgren funnels. The primary objective was to determine the life-cycle and ecology of *Ophyiulus pilosus* (Blower and Miller, 1974) and some aspects of its association or disassociation with *Julus scandinavius* (Miller, 1974). A population of *Cylindroiulus nitidus* occurs at the Derbyshire site and this has also been described (Blower and Miller, 1977). However, all the diplopods were sorted and characterized from each sample and, on several occasions, all the macrofauna. In this paper a preliminary description of the entire millipede fauna of each site is given and tentative steps taken towards defining and understanding some of the principles governing the structure of millipede associations.

The Sites and Their Faunas

The Welsh site is on the Gower peninsular by Llethrid and is variously known as Coed Abertawe or Park Woods (grid reference SS(21) 532910); this site will be referred to as Llethrid wood. It consists of oak (*Quercus* spp.) and sycamore (*Acer pseudoplatanus*) standards, coppiced hazel (*Corylus avellana* L.) and an understory of bramble (*Rubus fructicosus* L.) and ferns. Miller (1974) estimated an annual fall of litter of 420 g m^{-2}, mainly sycamore (245 g) and oak (140 g). There is a persistent cover of litter on the surface of a shallow soil with a mull-like moder humus form.

The Derbyshire site is an unnamed area of woodland just at the head of Mill Dale (grid reference SK(43) 152549) and will be referred to by this name. It

Table I. Densities per square metre and estimated biomass in milligrams fresh weight of overwintering populations

Mill Dale	1/4/68	9/72	20/10/75	17/10/77	Mean m^{-2}	Mean biomass mg
^{o} *Geoglomeris jurassica* Verhoeff			6		1	1
Glomeris marginata (Villers)	1	38			10	124
Microchordeuma scutellare (Ribaut)	16	62	50	64	48	70
^{o} *Polydesmus* spp.		42	2		11	16
Archiboreoiulus pallidus (Brade-Birks)			24	74	25	18
Julus scandinavius Latzel	21				5	147
Ophyiulus pilosus (Newport)	32	20	10	10	18	170
Cylindroiulus nitidus (Verhoeff)	56	116	54	190	104	855
Tachypodoiulus niger (Leach)	57	8	30	12	27	340
^{o} *Ommatoiulus sabulosus* (Linne)			2		*	2
Total Individuals m^{-2}	183	286	178	350	249	
Total Biomass mg m^{-2}	2769	1832	760	1594		1743

Llethrid	1/9/68	24/10/68	27/9/71	21/9/76	23/9/77	Mean m^{-2}	Mean biomass mg
Glomeris *marginata* (Villers)	24	32	12	16	13	17	1112
Microchordeuma *scutellare* (Ribaut)	28	38	24	52	109	54	74
° *Chordeuma* *proximum* (Ribaut)			6		11	3	18
° *Polymicrodon* *polydesmoides* (Leach)		1			3	1	*
° *Polydesmus* spp.		1	10	2	24	7	30
Brachydesmus *superus* (Latzel)	298	261	97	9	78	148	28
° *Proteroiulus* *fuscus* (Amstein)			2			*	*
Blaniulus *guttulatus* (Bosc)	26	52	197	212	333	164	66
Julus *scandinavius* (Latzel)			8	22	15	9	98
Ophyiulus *pilosus* (Newport)	390	241	319	530	214	339	2271
° *Cylindroiulus* *punctatus* (Leach)			13		21	7	31
Tachypodoiulus *niger* (Leach)	2	8	15	5	5	7	92
Ommatoiulus *sabulosus* (Linne)	2	9	23	1	2	7	163
Total Individuals m^{-2}	770	643	726	849	828	763	
Total Biomass, mg m^{-2}	4681	6394	2757	2857	3228		3983

* fractions of an individual or milligram omitted.

° "occasional" species.

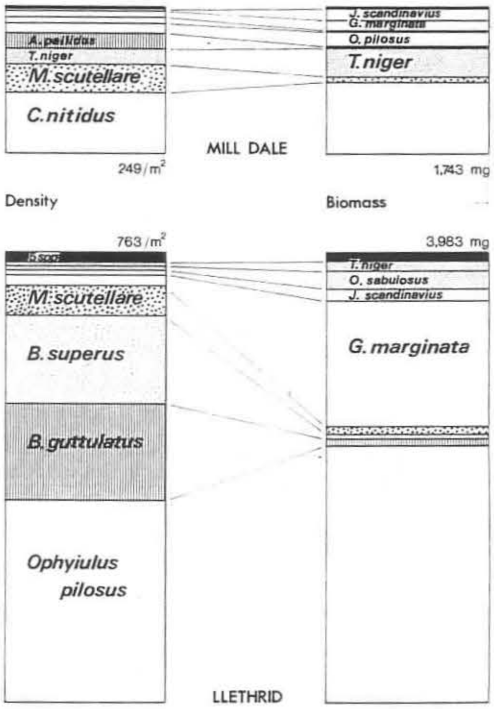

Fig. 1. Mean overwintering density and biomass of millipedes at Mill Dale and Llethrid. The means are derived from four separate years, the data for which is given in Table I. The top black portion of each column represents the occasional species (five at Llethrid, two at Mill Dale) listed in Table I.

consists of sycamore (*Acer pseudoplatanus*) and elm (*Ulmus glabra* Huds.) standards with an occasional yew (*Taxus baccata* L.), a well-spaced understory of elder (*Sambucus nigra* L.) and a patchy herb layer of lesser celandine (*Ranunculus ficaria* L.), nettle (*Urtica dioica* L.) and wood avens (*Geum urbanum* L.). Miller (1974) records a litter fall of 350 g m $^{-2}$, mainly of elm (213 g) and sycamore (123 g), most of which has disappeared by June leaving a bare soil which is a deep loam of typical mull form.

Each sampling area consists of a rectangle 10 × 20 m with its long axis rising up a slope. For certain reasons, a distinction has been made between an upper and lower 10 m square but for the present purpose reference will be made only to the fauna of the lower squares. At Mill Dale, ten units of 0·05 m $^{-2}$ of soil were taken on each occasion. At Llethrid, ten units of 0·10 m $^{-2}$ of litter and 0·05 m $^{-2}$ of soil beneath were taken.

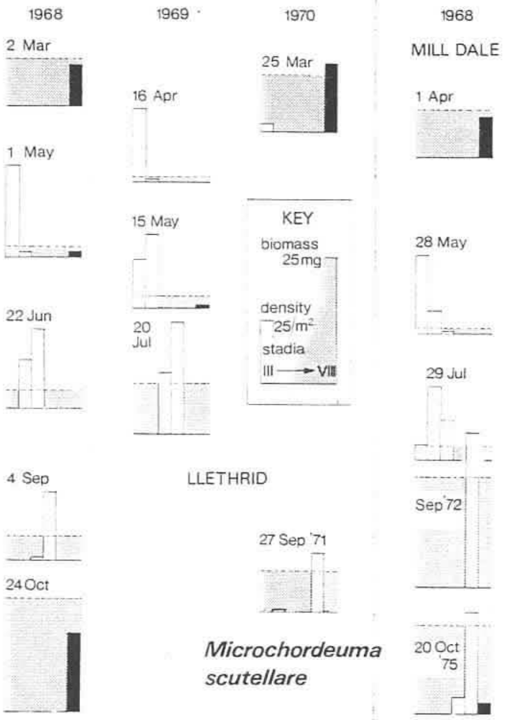

Fig. 2. Progression of stadia with date in *Microchordeuma scutellare*, at Llethrid and Mill Dale. Columns representing adults (stadium VIII) are black. The height of the stippled area indicates the biomass.

The fauna

Llethrid has a low density of lumbricid worms (24 m^{-2}) belonging almost exclusively to the pigmented species (*Lumbricus rubellus* Hoffmeister), which, on this site, appears to live near to the surface. At Mill Dale there is a much higher density (120 m^{-2}) of unpigmented subsurface species belonging to the genera *Allolobophora* and *Octolasion*. Both sites have rather sparse chilopod faunas, Llethrid with occasional specimens of *Lithobius variegatus*, *Strigamia acuminata* and *Haplophilus subterraneus*, Mill Dale with up to 50 m^{-2}, principally *Brachygeophilus truncorum*.

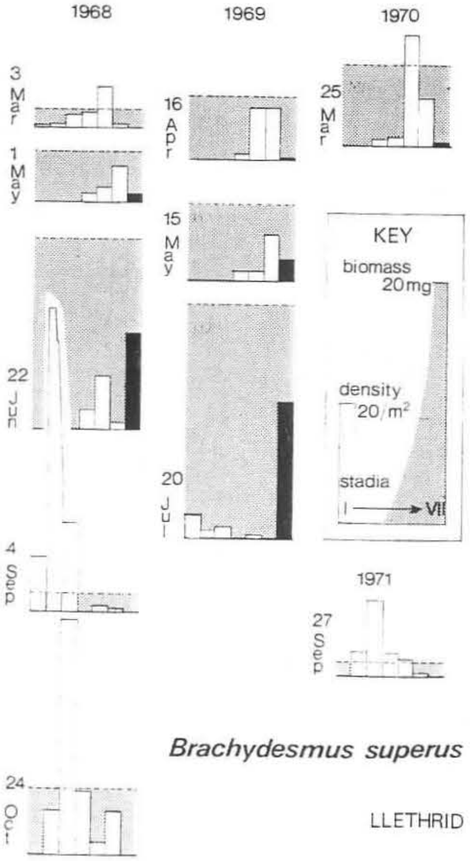

Fig. 3. Progression of stadia with date in *B. superus*. Columns representing adults (stadium VII) are black. Height of stipple indicates biomass.

The Millipede Associations

The mean densities of the millipedes forming the overwintering populations of four years are summarized in Table I and Fig. 1. Individuals of each species have been assigned to stadia and their age determined from the change in stadial composition over several samples during one or more years. The method and results for *Ophyiulus pilosus* and *Cylindroiulus nitidus* have been given by Blower and Miller (1974, 1977). Details for *Microchordeuma scutellare*, *Brachydesmus superus*, *Blaniulus guttulatus* and *Archiboreoiulus pallidus* are briefly given here and summarized in Figs 2, 3 and 4.

For each stadium of each species either the fresh weight or an estimate of

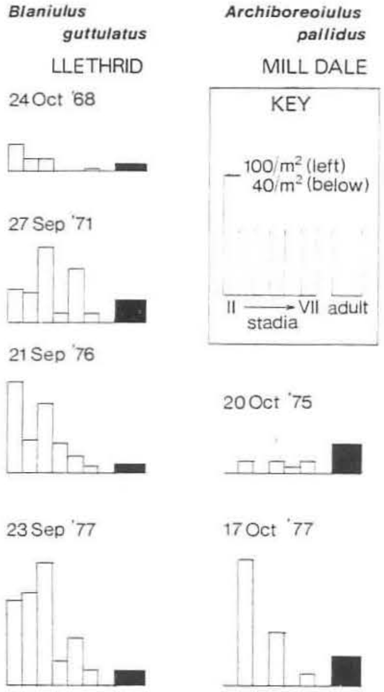

Fig. 4. Stadial structure of overwintering populations of the blaniulids for each year. The wide black column represents *all* adult stadia (VIII upwards). Note the vertical scale for *B. guttulatus* differs from that of *A. pallidus*.

volume derived from length and diameter using the formula $\pi r^2 l$, is available. For some stadia both fresh weights and volume estimates are available and these show the specific gravity to be sufficiently close to unity to permit either volume or weight to be used as estimates of biomass. Figure 1 shows that the average density at Llethrid is more than three times that at Mill Dale. Even when the average biomasses are compared, the advantage of the Llethrid association is only reduced to 2·3 times (see dotted extension of the Mill Dale biomass prism).

The relative contributions of the different species to the associations based on density is quite different from those based on biomass; the small species such as the blaniulids and *Brachydesmus superus* naturally contribute less biomass, but since they are represented mainly by younger stadia, their overall contribution is very small. In contrast, the larger species such as the ommatoiulines and *Glomeris marginata* are represented by a higher proportion of adults and appear much more prominently in the biomass prism. The biomasses of the numerically dominant species at each site, *O. pilosus* and *C. nitidus* confirm their dominance.

Grades of presence

There are four grades of presence within the associations:

(i) In similar numbers and mass from sample to sample and present in most of the units (quadrats) of each sample. This grade includes the dominant species on each site, *O. pilosus* and *C. nitidus* and the next most characteristic species at both sites, *Microchordeuma scutellare*, all with frequencies of 80–100% within each sample.

(ii) Showing a decreasing or increasing trend but with a high frequency in the samples in which they are more numerous. Included here are *Glomeris marginata* and *Brachydesmus superus* which are abundant in earlier Llethrid samples (see Table I) and *Blaniulus guttulatus* and *Archiboreoiulus pallidus*, which become abundant in later Llethrid and Mill Dale samples respectively (see Table I).

(iii) Present in all the samples but with lower density and frequency. Both ommatoiulines (*O. sabulosus* and *T. niger*) at Llethrid and *T. niger* at Mill Dale are present in the samples from all four years but never occur in more than half the sample units.

(iv) Species numerically unimportant, occupying few units in one or two of the samples. These are the species marked in Table I as "occasional" and represented in Fig. 1 by the upper black portions.

We can discount the fourth grade as of little importance to the associations. The third grade, constantly present but at low frequency, appears to consist of species that would be better considered as components of a larger association than that under consideration; their range appears to extend beyond the study area. Species in the second grade suggest that the character of the association has changed during the ten years, whereas species of the first grade appear to be associated with the unchanging aspects of the sites.

Age structure and life-cycle characteristics

There are two principal types of life-cycle represented, the semelparous species which breed once and then die, and the iteroparous species which survive several years as mature animals and breed in each of these. Semelparous species include *Julus scandinavius*, reaching maturity in three years, *Ophyiulus pilosus* maturing in two years and the true *annuals*, *Microchordeuma scutellare* and *Brachydesmus superus*, with trimodal, bimodal and unimodal age structures respectively. The life-cycles of the two semelparous julines *Julus scandinavius* and *Ophyiulus pilosus* were described by Blower (1970) and Blower and Miller (1974). The life-cycles of the two annual species are described in outline here (see Figs 2 and 3). The iteroparous species include *C. nitidus* (Blower and Miller, 1977), *T. niger* (Blower and Fairhurst, 1968), *O. sabulosus* (Halkka, 1958; Fairhurst, 1968) and *Glomeris marginata* (Heath *et al.*, 1974). The blaniulid species are also iteroparous. Details for *Blaniulus guttulatus* are given by Brookes and Willoughby (1978), and some further information on *B. guttulatus* and *A. pallidus* is included here (see Fig. 4). Iteroparous species may have an age structure including a relatively higher proportion of adults since these represent several generations. Nevertheless, the age structure of *C. nitidus* and the blaniulids at Mill Dale and Llethrid is still dominated by the immature stadia.

The annual species

Figure 2 shows the change in stadial spectrum with date for *M. scutellare* at Llethrid and Mill Dale. Egg-laying appears to be very early in the year, judging from the appearance of young stadia (III) by 16 April at Llethrid, and the complete absence of adults on this date. Stadium IV appears by 15 May, V by 22 June 1968, VI by 29 July 1969 and adults by the end of October at Llethrid. At Mill Dale stadia III and IV appear on 28 May, and by the end of July only a few have reached stadium V, compared with mid-July at Llethrid where stadia V and VI are present. Also, there are more individuals remaining in the penultimate stadium (VII) in October at Mill Dale. This slower development at Mill Dale does not seem in any way disadvantageous since similar densities are found from year to year in both northern and southern sites (see Table I).

Figure 3 shows the succession of stadia of *Brachydesmus superus* at Llethrid. In contrast to *M. scutellare*, egg-laying by this species appears to occur in late spring and summer; there are no early instars in the sample of 22 June, 1968. The sample of 20 July 1969 is the earliest to contain early instars and most adults are found in the June and July samples. The autumn populations (samples of 24 October, 1968 and 27 September, 1971) show peaks at stadium III, but in the 1968 and 1970 March samples the predominant stadium is V, suggesting development during the winter months.

In the biennial and triennial julines and in the iteroparous species there is no change in stadial spectrum during the winter months. In contrast, the annual species show evidence of winter activity, early egg-laying in *M. scutellare* and stadial progression in *B. superus*. These annual species show an interesting difference in the time they achieve their maximum biomass. *M. scutellare* attains its greatest biomass over the winter; *B. superus* achieves its maximum biomass in mid-summer (compare the areas of stipple in Figs 2 and 3).

The iteroparous blaniulids

Brookes and Willoughby (1978) suggest that *Blaniulus guttulatus* overwinters first at stadia II and III, secondly at IV and V and thirdly at VI and VII. The data assembled in Fig. 4 is not inconsistent with this pattern of life cycle; each of the autumn samples of 1971, 1976 and 1977 show clear peaks at stadium IV, the samples of 1971 and 1977 also show peaks at stadium VI. *A. pallidus*, in reasonable numbers at Mill Dale in the sample of autumn 1977 shows clear peaks at stadia III, IV and VII (see Fig. 4) and could, from this slender evidence, have a similar life-history to *B. guttulatus*.

Discussion

The earliest estimates of the size of millipede associations from woodland are those of Bornebusch (1930) for Danish sites. He records densities of 110 and 177 m^{-2} from oak and beech mull respectively and much lower densities for mor sites. Van der Drift (1951) describes an association of mainly two species from a Dutch beech wood, with raw humus, of 80 m^{-2}. More recently Dunger (1958) mentions densities rising to 200–300 m^{-2} in spring and autumn. In a mixed deciduous wood in Britain Blower (1970) found a mean density of 100 m^{-2} rising to 300 m^{-2} in some months. This last site had a moder humus and a very low pH (4–4·5).

Whilst the association at Mill Dale (average density 249 m^{-2}, varying from 183–350 m^{-2}) is as large as any previously described, that from Llethrid (mean density 763 m^{-2} varying from 643–849 m^{-2}) is far larger. Bornebusch (1930) provided the only estimates of biomass we possess, but his figures of 4·7 and 7·5 g m^{-2} for densities of 110 and 177 individuals m^{-2} seem rather high, and may be overestimates due to insufficient knowledge of the age or stadial structures of the populations.

The extraordinary abundance of millipedes at Llethrid might be correlated with the low density of lumbricid worms. It is possible that the millipedes at Llethrid are occupying the niche of the mull-forming worms which are unable to exist in the free-draining shallow soil at Llethrid. Blower (1974) has estimated that the population of *O. pilosus* at Llethrid could consume up to half the annual fall of sycamore leaves which themselves make-up a third of the total litter fall. Since *O. pilosus* accounts for only a third of the total millipede density or half of the biomass, it appears that the millipedes at Llethrid may consume a substantial part of the available detritus. Perhaps here at Llethrid we have the archetype of Muller's "Insect mull", if for "insects" we read "millipedes".

At Mill Dale all the leaf litter has disappeared by early summer; on what, therefore, do the millipedes rely for their food? Are they secondary consumers of detritus like the subsurface lumbricids, with which they co-exist, or are they feeding on root material?

The manner in which the several species of millipedes at each site partition the resources is a problem less immediate than that presented by the inter-site comparison discussed above, but it is important nonetheless. To discuss the partitioning of the main variable resources of food, space and time, the ommatoiulines often operate above the ground and may exploit sources of primary production, whereas *Glomeris marginata* and the julines can be seen to feed on litter at the surface, and there is the less direct evidence of the successful rearing of *O. pilosus* from egg to adult on a diet of sycamore leaves alone. Both julines, however, spend much of their time in the soil. It can be suggested that the blaniulids, like *C. nitidus*, are secondary exploiters of the detritus or feed on root material and that their share of the space is below the surface.

It is at present difficult to know how time is shared, but a number of considerations are relevant. The population of *O. pilosus* reaches its maximum biomass by autumn (about 2000 mg m^{-2} as compared with a mean value for the summer samples of 1300 mg m^{-2} (see Table I, and Blower and Miller, 1974). *M. scutellare* also attains its highest biomass during the winter months. In contrast, we have shown above that *B. superus* attains its maximum biomass by early summer. *O. pilosus* and *M. scutellare* may, therefore, need most of their food at the same time and presumably concentrate on different food items; *B. superus* may use the same resource and avoid competition temporally.

The relative proportions of the species at Llethrid in terms of biomass would differ markedly from the autumn plots in Fig. 1 if plotted from summer samples. The *O. pilosus* component would be reduced by nearly half and the *B. superus* component would be more than trebled. There are, unfortunately, fewer summer samples because the initial objective dictated that a long-term picture of the overwintering stadial spectrum was more important. Clearly, some concepts of community structure and knowledge of the population dynamics of the individual species are necessary before deciding which data to collect and how it should be marshalled in a meaningful manner.

It is tempting to suggest that the relatively dry summers of 1975 and 1976 were responsible for the decrease in abundance of *G. marginata* because it feeds at the surface, and of *B. superus* since this species makes its maximum demands on the food supply in the summer months. However, I am quite unable to offer any good reason for the concurrent increase in abundance of the two blaniulids. The inverse relationship between the densities of *B. superus* and

B. guttulatus at Llethrid is very interesting, considering the two are often associated in garden and arable land.

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